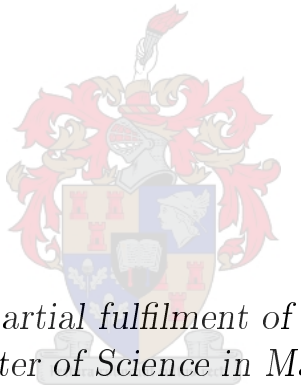
Complex life cycle and biphasic range expansion in plants.

by

Tremaine Robertson



Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Mathematics in the Faculty of Science at Stellenbosch University

Supervisor: Prof. Cang Hui

Co-supervisor: Dr. Guillaume Latombe, Dr. James Rodger, Dr. Pietro Landi

March 2020

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Date: .....March 2020.....

Abstract

Complex life cycle and biphasic range expansion in plants.

T.W. Robertson

Department of Mathematics,
University of Stellenbosch,
Private Bag X1, Matieland 7602, South Africa.

Thesis: MSc (Mathematics)

March 2020

The rate of the spread of populations into new habitat has been extensively studied. In particular, the long-term spread rate of plant populations has been analytically formulated in terms of the travelling wave solution. However, plants often display a biphasic range expansion, where a long-term fast spread phase is preceded by a slower spread phase. This has been explained by fat-tailed dispersal kernels, habitat transition or stratified diffusion. Nonetheless, since pollen production and dispersal are integral parts of the plant life cycle, they might play a role in the spread patterns of plants. For these reasons, I included pollen production and dispersal, in addition to seed production and dispersal, in an integrodifference equation (IDE model of plant spread in continuous space and discrete-time. The numerical results showed that biphasic range expansions are produced by considering the complex life cycle of plants. Furthermore, I observed that seed dispersal increased both the slow and fast phases of the biphasic range expansion. Pollen dispersal had constrained the velocity of the slow phase, but drove the velocity of the fast phase. However, when pollen dispersal is much higher than seed dispersal, a boom-and-bust phenomenon is observed, indicating that the velocity of spread decreases and the population declines and eventually goes extinct as few plants are located at far distances to be pollinated. These results shed new light on the importance of different life stages and dispersal events in driving biphasic range expansions of plant populations.

Uittreksel

Komplekse lewensiklus en tweefasige uitbreiding in plante.

("Komplekse lewensiklus en tweefasige uitbreiding in plante.")

T.W. Robertson

Wiskunde departement,
Universiteit van Stellenbosch,
Privaatsak X1, Matieland 7602, Suid Afrika.

Tesis: MSc (Mathematics)

Maart 2020

Die tempo van die verspreiding van bevolkings na 'n nuwe habitat is breedvoerig bestudeer. In die besonder is die langtermynverspreidingsyfer van plantpopulasies analities geformuleer in terme van die bewegende golfoplossing. Plante vertoon egter dikwels 'n tweefase-uitbreiding, waar 'n langtermynverspreidingsfase voorafgegaan word deur 'n stadiger verspreidingsfase. Dit word verklaar deur vetstert waarskynlikheidsverdelings, habitatoorgang of gestratifiseerde diffusie. Aangesien stuifmeelproduksie en verspreiding integrale dele van die plantlewensiklus is, speel dit egter 'n rol in die verspreidingspatrone van plante. Om hierdie redes het ek stuifmeelproduksie en verspreiding, benewens saadproduksie en verspreiding, ook in 'n model met 'n integraaldifferensiaalvergelyking (IDV van plantverspreiding in kontinue ruimte en diskrete tyd ingesluit. Die numeriese resultate het getoon dat die uitbreiding van tweefasige omvang geproduseer word deur die ingewikkelde lewensiklus van plante. Verder het ek opgemerk dat verspreiding van saad 'n positiewe uitwerking op beide die stadige en vinnige fases van die uitbreiding van die bifasiese reeks het. Stuifmeelverspreiding het 'n negatiewe uitwerking op die snelheid van die stadige fase, maar 'n positiewe invloed op die snelheid van die vinnige fase. Wanneer die stuifmeelverspreiding egter veel hoer is as die verspreiding van saad, word 'n styg-en-daal verskynsel waargeneem, wat aandui dat die verspreidingsnelheid daal en die bevolking daal en uiteindelik uitsterf. Hierdie resultate werp nuwe lig op die belangrikheid van verskillende lewensfases en verspreidingsgebeurtenisse in die bevordering van die uitbreiding van plantegroei in tweefase.

Acknowledgements

I would like to express my sincere gratitude to following people and organisations: Prof. Cang Hui (main supervisor), Dr. James Rodger, Dr. Pietro Landi and Dr. Guillaume Latombe (cosupervisors)and the National Research Foundation (NRF) and Stellenbosch University for funding my research over the past two years.

Contents

Declaration i

Abstract ii

Uittreksel iii

Acknowledgements iv

Contents v

List of Figures vii

1 Introduction 1

2 Model and Methods 6
2.1 The Integro-Difference Equation model 6
2.2 Analytical analysis 11
2.3 Numerical analysis 11

3 Results 13
3.1 Analytical solution 13
3.2 Numerical results 15

4 Discussion 20
4.1 Discussion 20

Appendices 24

A Supplementary figures 25
A.1 Range expansion and velocity of spread 25
A.2 Histograms for a wide range of σ_p and σ_s. 26
A.3 27
A.4 28
A.5 Sensitivity analysis with a detection threshold of $l^* = 0.95$ and each of the parameters in table 3.1. 29
A.6 MATLAB code for Fig. A.1 A and B 30

A.7 MATLAB code for Fig. 3.3 A - D. 34

List of References **41**

List of Figures

2.1 **The modelled plant life cycle used to determine the effect of pollen and seed dispersal on invasion dynamics.** Each plant l produces α pollen grains. The pollen, p, disperse through the dispersal kernel, k_p. Recipient plants use the pollen after dispersal, p_D, to produce seeds, s, where we assume that β is the maximum number of ovules per plant in our simplified model. Seeds disperse through the dispersal kernel, k_s, and dispersed seeds, s_D, will germinate with probability r or otherwise contribute to the seed bank. Seeds in the seed bank also germinate with probability r or otherwise survive in the seed bank with probability γ_s. Plants survive to the following year with probability γ. 8

3.1 **The three phases of the range expansion of a plant population.** Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9, \sigma_p^2 = 50, \sigma_s^2 = 80$ and initial population sizes $s_B(0,0) = 100, l(0,0) = 2$. B shows a boom-and-bust phenomenon. The detection threshold, l^*, is 1. These simulations are based on equations 2.1 to 2.6. 15

3.2 **Frequency distributions of the velocity under different initial conditions and dispersal abilities**. Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$, but $\sigma_p = 50$ and $\sigma_s = 80$ in A and B, and $s_B(0,0) = 100$ and $l(0,0) = 2$ in C and D. (A)-(B): Different initial conditions and (C)-(D): Different dispersal abilities. The detection threshold is 1. Each black arrow indicates the bin associated with the lag, slow and fast phase. 16

3.3 **The effect of pollen and seed dispersal ability on the duration of the lag and slow phase, and the velocity of the slow and fast phase to the changes in the pollen and seed dispersal ability.** Parameter values were $r = 0.2, \alpha = 650, \beta = 20, \mu = 0.002, K = 20, \gamma_s = 0.94, \gamma_l = 0.89$. The grey and black regions respectively represent boom-and-bust and extinction, whereas the blue-yellow region represents biphasic range expansion. 17

3.4 **Parameter sensitivity when each of the parameters is increased by 5%.** The sensitivity measures the proportion of change in the parameter values when they are increased by 5% with respect to those in Fig. 3.1. Shown is the sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phase. For this analysis, the duration of the lag phase did not change. 19

A.1 **Range expansion and spread rate for different detection thresholds**. Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$. The slow phase is sensitive to the detection threshold, but not the fast phase or asymptotic spread rate. 25

A.2 **Histogram plots for $\sigma_p = 10 : 10 : 100$ and $\sigma_s = 10 : 10 : 100$.** Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$. These histograms validate the existence of the slow phase. Horisontal axis: velocity and vertical axis: frequency. 26

A.3 27

A.4 28

A.5 **Parameter sensitivity when each of the parameters is decreased by 5% and the detection threshold, l^*, is 0.95.** The sensitivity measures the proportion of change in the parameter values when they are decreased by 5% with respect to those in Fig. 3.1. Shown is the sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phase. For this analysis, the duration of the lag phase did not change. Only γ_l, the plant survival rate, increased the duration of the lag phase. The decrease of 5% of the detection threshold and decrease of 5% in γ_s resulted in an almost 200% longer duration of the slow phase. The 5% decrease in γ_l and the detection threshold resulted in a staggering 600% increase in the duration of the lag phase and a 100% decrease in the spread rate of the slow phase. 29

Chapter 1

Introduction

Biological invasions have attracted increasing attention over the years. The number of new alien species has been increasing steadily since the 1800s and shows no sign of saturation (Seebens *et al.*, 2017). An invasive species is, by definition, an alien species with self-reproducing populations over multiple life cycles that produce offspring at significant distances from the introduction site (Hui and Richardson, 2017). Invasive species can have an impact on the environment, economy and health (Hui and Richardson, 2017). Modelling the spread of invasive species is therefore an integral part of ecological theorisation and has immediate applications in understanding and forecasting the range dynamics of species across large geospatial scales (Clark, 1998), including biological invasions and the range shifts of species in response to climate change (Shigesada *et al.*, 1996). Predicting the velocity of the spread of species is therefore paramount to the preventional and proactive management of invasive species (Bullock *et al.*, 2008) in yet to be invaded areas (Lucie Hemrová, 2017).

Invasion dynamics are typically characterised by three stages: (i) an establishment stage after introduction during which no range expansion is detectable (also called the lag phase), (ii) a range expansion stage, in which the occupied area continuously expands and (iii) the saturation stage when all niches have been filled up and range expansion ceases (Shigesada *et al.*, 1996). We are interested in the invasion dynamics of the first two stages. The lag phase occurs when the expansion is pinned down from Allee effects, (Stephens *et al.*, 1999)), maladaptation (Crooks *et al.*, 1999) or not being detected (Shigesada *et al.*, 1996). However, the duration of the lag phase is often difficult to predict, making the invasion and outbreaks of many introduced species a surprise to managers. Better mathematical formulation of the lag phase could bring more accurate estimates of the invasion debt caused by these already introduced species but yet to spread (Rouget *et al.*, 2016).

The rate of spread is not constant during the expansion stage, with a biphasic range expansion often observed that consists of an initial slow phase followed by a fast phase of spread (Shigesada *et al.*, 1996). For instance,

the spread of common starlings, *Sturnus vulgaris*, in North America (Okubo, 1988). After a lag phase of 10 years after 160 birds were introduced in New York in 1880, the range expansion started with a slow linear velocity of 11.2km/yr between 1900 and 1915, followed by a fast linear velocity of 51.2km/yr between 1915 and 1950. Three explainations have been conjectured. First, the faster velocity of common starlings in North America is believed to be a result of invasion over the prairie, where fewer food sources and towns are available compared to the timbered east in the slower expansion phase (Okubo, 1988). Moreover, temporal variations in habitat conditions could also trigger biphasic range expansion. For example, in map butterflies, the transition from a slow first phase to a faster second phase could be explained by increased temperatures from 1999 that resulted in maximal annual dispersal and velocity (Mitikka *et al.*, 2008). Further studies on species with complex life cycles like the cotton bollworm, *Helicoverpa armigera*, in East-Asia (Ouyang *et al.*, 2014), and the rose chafer beetle, *Oxythyrea funesta*, in central Europe (Horak *et al.*, 2013), also propose that climate change and human activities are the drivers of biphasic range expansion. Habitat transition is thus considered as the driver of the spread switching from a slower to a faster phase.

Dispersal is the movement of individuals from their natal sites to a new site of potential habitation (Nathan *et al.*, 2012). The dispersal distance is the distance between the starting and the ending locations of a dispersal event and a building block of the spreading process. The probability distribution of dispersal distances for a focal population is called the dispersal kernel, which can be thin-tailed (e.g. negative exponential kernel) or fat-tailed (e.g. a truncated power-law kernel). Fat tails decrease slower than that of any negative exponential kernel and are characterised by a comparatively high frequency of long-distance dispersal (LDD) events (Nathan *et al.*, 2008).

It has been shown that fat-tailed dispersal kernels can produce accelerating range expansion, which visually resembles, often statistically indistingualable from, the biphasic expansion with a faster spreading phase after a slower initial phase (Kot *et al.*, 1996; Nathan *et al.*, 2001). For instance, records of range expansion in South Africa after releasing 18 birds in Cape Town in 1897 (Harrison and Cherry, 1997) also disclosed a biphasic range expansion: a 6.1 km/yr linear expansion before 1940 and a faster linear expansion phase of 25.7 km/yr post-1940 (Hui *et al.*, 2012). A power-law fat-tailed dispersal kernel, $(d) \sim d^{-1.5}$, was reported as a likely explanation for the biphasic range expansion of starlings (Hui *et al.*, 2012). Therefore, fat-tailed dispersal kernels have been considered as the second candidate explanation for biphasic range expansion.

The stratified diffusion serves as the third candidate explanation for the biphasic expansion (Shigesada *et al.*, 1996). Species experiensing a stratified dispersal process often undertake both neighbourhood short-distance diffusion and long-distance dispersal simultaneously. Neighbourhood diffusion marks the initial range expansion. While the founder population expands its range,

long-distance individuals create new satellite colonies that increase in numbers, resulting in a faster phase of expansion when the founder population coalesced with satellite populations (Shigesada *et al.*, 1996). The expansions of the English Sparrow and House Finch also consist of an initial establishment phase followed by slow rate of expansion and then a faster and linear expansion in the third phase (Okubo, 1988), which have also been explained according to the stratified dispersal process. Stratified dispersal can also be caused by dispersal due to different vectors (e.g. natural and human-mediated dispersal like trade and transportations by humans (Hulme, 2009; Hiddink *et al.*, 2015) are both responsible for the invasion of many species).

Many invasive species that grow and expand their ranges might undergo a sudden decline in their densities (Simberloff and Gibbons, 2004), a phenomenon known as the boom-and-bust pattern, in which case the species settles at a significantly lower density after the boom-and-bust (Williamson and Griffiths, 1996). One explanation for this boom-and-bust pattern is environmental conditions, e.g. favourable weather, that cause the boom phase with the invasion dynamics returning to the bust phase when the environmental conditions inhibit establishment when they revert to their normal levels. Fast population growth that exceeds the carrying capacity and subsequently declines to its true equilibrium is a density-dependent explanation for the boom-and-bust patterns (Groves, 2006). Other explanations have connected this pattern to the reduction of the rescue effect in populations dynamics, e.g., metapopulations, from an extreme immigration rate. High emigration rates could have a negative effect on the population dynamics (Simberloff and Gibbons, 2004). If the probabilities of emigration from favourable and unfavourable habitats are balanced, then the rescue effect can maintain the range expansion. If the emigration from favourable patches is low, it may be insufficient to prevent populations in unfavourable patches from becoming extinct if only a small proportion of the habitat favours population growth. On the other hand, high emigration from only favourable patches, can result in a decline in rescuing individuals and result in a lower velocity of spread or even population extinction after a boom-and-bust pattern (Ramanantoanina and Hui, 2016).

Adaptive biotic interactions is another potential reason for the boom-and-bust phenomenon in invasive species. For example, plant species introduced into a habitat attract predators and pathogens over time (Hawkes, 2007; Wingfield *et al.*, 2011), and, as time progresses, predator efficacy can increase when native predators adapt to invasive prey (Carlsson *et al.*, 2009).

Species must undergo both reproduction and dispersal to expand their ranges (McGeoch and Latombe, 2016). A minimal model of range expansion involves positive population growth and dispersal. Positive population growth occurs when organisms complete their life cycles through survival, growth and reproduction at sufficiently high rates that the population increases over time (Kot *et al.*, 1996). Range expansion therefore can be limited by dispersal or life cycle processes, such as reproduction and dispersal of pollen and seeds in

plants. For species with a complex life cycle, the transition between specific life stages could serve as a *gear box* that controls the range expansion at different velocities. The range expansion will experience different gears when speeding up, due to specific transitions in the life cycle sequentially becoming the constraint, forming a step-wise transcient dynamics of acceleration towards the final asympototic rate of spread. This can be another possible explanation for biphasic range expansion and boom-and-bust phenomena. The growth of different life stages and dispersal could be limited by the life cycle in organisms with complex life histories: if the population growth is fast during expansion, then the velocity depends more on dispersal, but if the population growth is slow, then the velocity depends more and the growth dynamics of the population (Kot *et al.*, 1996), which might also become negative due to Allee effects.

The influence of seed dispersal on plant spread has been well documented in the literature (Higgins and Richardson, 1999; Bullock *et al.*, 2008; Malanson and Rodriguez, 2018). However, these models assume that all individuals reproduce equally well after dispersal and lack the explicit influence of pollen production and dispersal on plant spread. Wind-dispersed pollen obeys a leptokurtic dispersal kernel (Gleaves, 1973), that is, the number of seeds produced by pollen-receiving plants declines significantly with distance from the donor plants (Allison, 1990). This means that pollen receipt, and therefore seed production, is much lower for plants at low density (Allison, 1990; Starfinger and Stöcklin, 1996). This phenomenon is an example of an Allee effect, which is defined as a positive relationship between individual fitness and population density or population size (Allee, 1931).

A strong Allee effect causes a negative per capita growth rate when the population drops below a certain threshold and can therefore result in population extinction, and a weak Allee effect causes a reduced, but always positive, per capita growth rate when the population density is low (Wang and Kot, 2001). For example, the role of pollen limitation in an invasive estuarine grass, *Spartina Alterniflora*, was investigated with a varying supplementation of pollen and exclusion experiments in high population density areas and at the edge of the invasion where population density is low. Pollen deposition rates on stigmas and pollen traps were quantified along a windward to a leeward gradient. The edge of the invasion, where population density is low, exhibited pollen impoverishment that resulted in an 8-fold reduction in the number of seeds. Nine times more pollen was found on the stigmas of plants with a high density than those of low-density plants. The numerical results, which do not use dispersal kernels, showed that the delay of significant seed production caused by the limited supply of pollen persisted for decades until vegetative growth coalesced plants into continuous meadows, and this Allee effect has slowed the invasion rate (Davis *et al.*, 2004).

Furthermore, the incorporation of an Allee effect into an IDE, an integral equation that incorporates the dispersal and growth dynamics of populations (Kot *et al.*, 1996), may reduce the velocity of a species. For instance, an Allee

effect was incorporated into an IDE model with the growth and dispersal of a population in synchrony. A comparison between the IDEs with and without an Allee effect showed that the presence of the Allee effect resulted in a lower velocity of population spread (Kot *et al.*, 1996).

Limited pollen supply at the edge of the range expansion could result in an emergent Allee effect, which could constrain the rate of spread (Kot *et al.*, 1996). Previous models of spread are phenomenological. However, a mechanistic model incorporating pollen dispersal may provide new insights on the range expansion and velocity of plant spread. Also, previous models considering Allee effects focused only on asymptotic velocity (Kot *et al.*, 1996). However Allee effects could also affect the lag phase and create biphasic range expansion because velocity could initially be limited by population growth/seed production and then be limited by the dispersal kernel. Therefore, the explicit incorporation of pollen dispersal in plant spread models is more realistic and could provide more accurate results for predicting plant spread. For these reasons, we constructed a mathematical model in continuous space and discrete-time that accounts for the production and dispersal of pollen and seeds through integrodifference equations (IDEs), the recruitment of seeds into a seed bank and plant recruits. In addition to this, we simulated the range expansion and instantaneous and asymptotic velocity of a hypothetical plant species that is self-incompatible. These simulations were used to gain insight into how pollen production and dispersal, in addition to seed production and dispersal, influence different phases of range expansion, possible boom-and-bust phenomena, and the asymptotic spread rate of plants.

Chapter 2

Model and Methods

2.1 The Integro-Difference Equation model

A common mathematical paradigm for modeling the dispersal of species hinges on the random walk approximation (Brownian-motion), which yields a partial differential equation (PDE), also called a reaction-diffusion equation (Okubo, 1980). PDEs were first used in 1951 to model species invasions in continuous space and time, e.g. the reaction-diffusion model, where the reaction and diffusion terms represent recruitment and dispersal respectively (Skellam, 1951). These models assume that dispersal is governed by a Gaussian dispersal kernel (Williamson *et al.*, 2005), and yields travelling wave solutions, that is, a wave that moves in a certain direction while maintaining its shape (Kot *et al.*, 1996), with an asymptotic velocity of $c = 2\sqrt{rD}$, where r is the per-capita population growth rate, given by $r = F'(N)|_{N=0}$, where $F(N)$ is the reaction term and D represents diffusion (Skellam, 1951; Fisher, 1937). For example, PDEs were used to model the spread of oaks in England after the glacial period. The model showed that dispersal by rooks increased the diffusion of seeds and, consequently, the velocity of oaks (Skellam, 1951).

Since $c = 2\sqrt{rD}$ hinges on Brownian-motion, it may fail to realistically represent the velocity of the spread of a population. For example, seed dispersal typically disobeys Brownian-motion diffusion as a large number of seeds can be dispersed over large distances resulting in a fat-tailed dispersal kernel and is frequently studied by using integrodifference equations (Kot *et al.*, 1996). Furthermore, accelerated growth of the population in the model can result in an arbitrarily large asymptotic velocity. A remedy to this problem is to substitute the PDE model with an integral differential equation (Branco *et al.*, 2007). Integral differential equations in discrete time and continuous space are called integrodifference equations (IDEs) and can accommodate various demographic processes and dispersal kernels to approximate the velocity of species for any dispersal kernel (Weinberger, 1982; Kot *et al.*, 1996; Lewis *et al.*, 2016). For example, an integrodifference equation model that incorporates field es-

timates of seed dispersal and population growth dynamics was used to show that compatibility exists between dispersal data and the rapid spread of trees. The IDE model showed that rapid spread (more than 1000 m/year) of trees at the end of the Pleistocene is possible if, regardless of short average dispersal distances, the dispersal kernel is fat-tailed (Clark, 1998).

Plant species that have been introduced and settled in ecosystems have the potential to spread and increasingly occupy an ecosystem. Mortality, fecundity, habitat heterogeneity, dispersal barriers, vectors (e.g., wind and animals) and gravity/explosion are critical components of population demography that influence the spread of plant populations (Hui and Richardson, 2017). Plant range expansion can be constrained if plant life cycles are incomplete. The life cycle of plants starts with pollination, which is the transfer of pollen grains produced on the anther of a flower to the stigma by pollinators such as wind and insects. If this happens on the same flower or on the same plant, it is called self-pollination; otherwise, it is called cross-pollination. Recipient plants use the pollen to produce seeds. Seeds are dispersed by animals, water or wind from the parent plant. Seeds that settle in favourable ground germinate and grow into adult plants (Ashman *et al.*, 2004). In particular, pollen and seed dispersal by animals or wind are crucial in plant recruitment (Howe *et al.*, 1988). Limited pollen or seed supply at the front of the expansion can constrain the rate of spread. These two modes of dispersal represent stratified dispersal.

The amount of seeds that plants produce depends on the amount of pollen that they receive (Ashman *et al.*, 2004). The survival of plant populations in the landscape may therefore rely on the movement of their pollinators. Harvesting by humans, an increase in the number of plant herbivores and habitat fragmentation, among other factors, can cause a reduction in plant density, which may reduce pollination success.

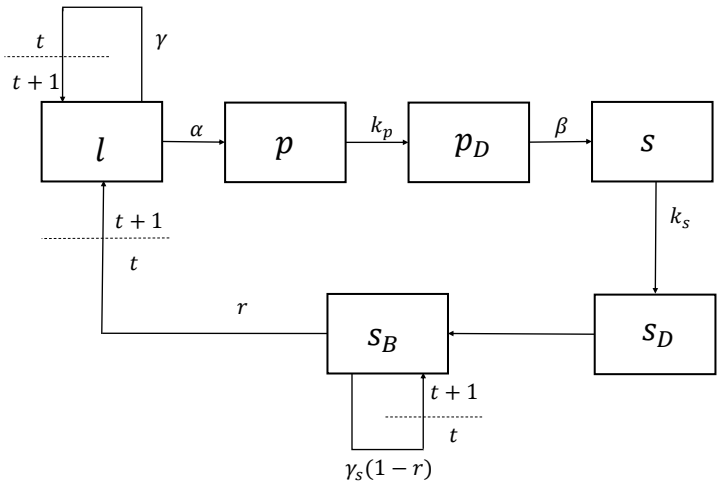


Figure 2.1: **The modelled plant life cycle used to determine the effect of pollen and seed dispersal on invasion dynamics.** Each plant l produces α pollen grains. The pollen, p, disperse through the dispersal kernel, k_p. Recipient plants use the pollen after dispersal, p_D, to produce seeds, s, where we assume that β is the maximum number of ovules per plant in our simplified model. Seeds disperse through the dispersal kernel, k_s, and dispersed seeds, s_D, will germinate with probability r or otherwise contribute to the seed bank. Seeds in the seed bank also germinate with probability r or otherwise survive in the seed bank with probability γ_s. Plants survive to the following year with probability γ.

I modelled the spread of a plant species in which seed production is determined by pollen dispersal. Let $l(x,t)$ be the number of plants at location x and time t. If we let α be the pollen production per plant, then the pollen produced at location x during year t is

$$p(x,t) = \alpha l(x,t). \tag{2.1}$$

The dispersal of pollen is mediated by a dispersal kernel, $k_p(x,y)$, which denotes the probability of pollen transfer from location y to location x (Kot *et al.*, 1996). Here, we assume an homogeneous habitat in which dispersal is independent on density. The dispersal kernels are

$$k_p(d) = \frac{1}{\sqrt{2\pi\sigma_p^2}} e^{-\frac{d^2}{\sigma_p^2}},$$

with variance σ_p^2, for pollen dispersal, and a Gaussian dispersal kernel,

$$k_s(d) = \frac{1}{\sqrt{2\pi\sigma_s^2}} e^{-\frac{d^2}{\sigma_s^2}},$$

with variance σ_s^2, for seed dispersal, where $d := |x - y|$. σ_p and σ_s are henceforth referred to as the dispersal ability of pollen and seeds respectively. The assumption of no pollen and seed loss during dispersal ensures that

$$\int_{-\infty}^{\infty} k_p(d)dy = 1$$

and

$$\int_{-\infty}^{\infty} k_s(d)dy = 1.$$

So, the pollen at location x after dispersal is

$$p_D(x,t) = k_p(x,x)p(x,t) + \sum_{\forall y \neq x} k_p(x,y)p(y,t). \tag{2.2}$$

where $k_p(x,x)$ is the proportion of pollen that remains at location x, and $\sum_{\forall y \neq x} k_p(x,y)p(y,t)$ is the dispersal of pollen from other discretized locations to location x. I used a Gaussian dispersal dispersal because it is the simplest and, more importantly, because fat-tailed dispersal kernels have already been proposed as a candidate explanation for biphasic range expansion.

I assume that self-incompatibility does not impact seed production, and that pollen grains are homogeneously distributed over the plants at every location, such that the probability of an ovule being pollinated is given by $1-\exp\left(-\frac{\mu p_D(x,t)}{\beta K}\right)$, where β is the maximum number of ovules per plant and μ is a parameter that describes the efficacy of pollination. Hence, the seed production at location x is

$$s(x,t) = \beta l(x,t)\left(1 - e^{-\frac{\mu p_D(x,t)}{\beta K}}\right), \tag{2.3}$$

that is, the Skellam function for the recruits of a single-species population (Skellam, 1951). Some of these seeds are dispersed by vectors such as wind or animals (Schurr *et al.*, 2018), such that the number of seeds after dispersal is

$$s_D(x,t) = k_s(x,x)s(x,t) + \sum_{\forall y \neq x} k_s(x,y)s(y,t), \tag{2.4}$$

where $k_s(x,x)$ is the proportion of seeds that remains at location x, and $\sum_{\forall y \neq x} k_s(x,y)s(y,t)$ is the dispersal of seeds from other locations.

The proportion of seeds that germinates at location x during the year t from either dispersal or seed bank is given by r. Seeds that do not germinate can survive in the seed bank until the following year with probability of γ_s, that is,

$$s_B(x,t+1) = \gamma_s(1-r)[s_B(x,t) + s_D(x,t)]. \tag{2.5}$$

Assuming that the seeds in the seed bank at every location are homogeneously distributed, the probability of seed recruitment at location x is

$$1 - e^{-\frac{r[s_B(x,t)+s_D(x,t)]}{K}}.$$

Each location x has K sites that can accommodate a single plant. Thus, the number of recruits is limited by the space available. If γ is the survival rate of plants from year t to year $t+1$, and $l(x,t)$ the number of adult plants at location x during year t, then the potential plant growth at location x during year $t+1$ is $K - \gamma l(x,t)$. Assuming the absence of competition among seeds in the seed bank, the number of plants recruited from seed germination is

$$\left(1 - e^{\frac{-r[s_B(x,t)+s_D(x,t)]}{K}}\right)(K - \gamma l(x,t)).$$

The number of plants at location x that survive from year t to year $t+1$ is given by $\gamma l(x,t)$. Therefore, the total number of adult plants at location x during year $t+1$ is

$$l(x,t+1) = \left(1 - e^{-\frac{r[s_B(x,t)+s_D(x,t)]}{K}}\right)(K - \gamma l(x,t)) + \gamma l(x,t)$$

which is equivalent to

$$l(x,t+1) = K - (K - \gamma l(x,t))e^{-\frac{r[s_B(x,t)+s_D(x,t)]}{K}}. \tag{2.6}$$

The system of equations in continuous space and discrete-time is

$$p(x,t) = \alpha l(x,t) \tag{2.7a}$$
$$p_D(x,t) = \int_{-\infty}^{\infty} k_p(x-y)p(y,t)dy \tag{2.7b}$$
$$s(x,t) = \beta l(x,t)\left(1 - e^{-\frac{\mu p_D(x,t)}{\beta K}}\right) \tag{2.7c}$$
$$s_D(x,t) = \int_{-\infty}^{\infty} k_s(x-y)s(y,t)dy \tag{2.7d}$$
$$s_B(x,t+1) = \gamma_s(1-r)[s_B(x,t) + s_D(x,t)] \tag{2.7e}$$
$$l(x,t+1) = \left(1 - e^{-\frac{r[s_B(x,t)+s_D(x,t)]}{K}}\right)(K - \gamma l(x,t)) + \gamma l(x,t) \tag{2.7f}$$

2.2 Analytical analysis

My initial model was a system of partial differential equations (PDEs) that described the instantaneous rate of change of pollen, seeds and plants with respect to time t. The PDEs with the pollen and seeds contained diffusion terms for pollen and seeds. I derived the travelling wave solution or asymptotic velocity of the plants. However, the result contained the diffusion term for seeds and not pollen. Since I was interested in an analytical solution that contains both pollen and seeds, I redesigned the model with continuous space and discrete time. The model, as shown above, accounts for pollen production, pollen dispersal through an integrodifference equation with a Gaussian distribution, seed production, seed dispersal through an integrodifference equation with a seed dispersal kernel, a seed bank and plant growth. I attempted to derive an analytical formula for the asymptotic velocity of the spread of plants, but the full model is not analytically tractable. Therefore, I considered a simplified case of unlimited pollination and limited seed dispersal, and obtained a result similar to the travelling wave solution in the literature (see equation (3.9)). This is to confirm that the part of my model that deals with only seed dispersal yields a traveling wave solution consistent to what is reported in the literature.

2.3 Numerical analysis

As an analytical solution was not available for the full model, I implemented simulations in MATLAB to study the consequences of pollen and seed dispersal ability for range expansion. To do so, I discretised the continuous kernels over a linear landscape of length L by dividing it into N equal subintervals. In these simulatios I assessed range expansion by assessing range position at each time step. The instantaneous velocity at time t were calculated as $c = x^*(t+1) - x^*(t)$, where $x^*(t)$ is the position of the range front for a certain detection threshold l^*, that is, $x^*(t) = \max\{x \geq 0 : l(x,t) \geq l^*\}$.

To assess different phases in range expansion, I studied the frequency distribution of instantaneous velocities during the spread. Such frequency distribution is approximated with histograms. Each histogram has 15 bins and depict the lag, slow and fast phase of the range expansion under different initial conditions and dispersal abilities (Fig. 3.2). The asymptotic or fast phase velocity was the highest velocity of each of the range expansion curves. Hence, I chose the velocity of the fast phase as the maximum velocity. By disregarding the largest and smallest velocities in each of the histograms, I identified the velocity of the slow phase by choosing the velocity with maximum frequency; if more than one such velocity existed, I chose the one that corresponded to the minimum velocity. The frequency of the velocity was used as the duration of the phases associated with them. The histograms were used to confirm the

existence of the slow phase observed in Fig. 3.1.

I generated heat maps to investigate the sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phases to changes in the pollen and seed dispersal abilities. I varied each of the remaining parameters individually to investigate their influence on the duration of the lag and slow phase, and the velocity of the slow and fast phase. I used $l^* = 1$ in these simulations.

Chapter 3

Results

3.1 Analytical solution

A travelling wave is a wave that moves in a certain direction while maintaining its shape (Kot *et al.*, 1996).

An analytical solution for the full model is not available. However, I derived a travelling wave solution for a simpler version of the model. Disregarding the seed bank and assuming unlimited pollination, the model reduces to

$$s(x,t) = \beta l(x,t) \tag{3.1a}$$

$$s_D(x,t) = \int_{-\infty}^{\infty} k_s(x-y)s(y,t)dy \tag{3.1b}$$

$$l(x,t+1) = \left(1 - e^{-\frac{rs_D(x,t)}{K}}\right)(K - \gamma l(x,t)) + \gamma l(x,t) \tag{3.1c}$$

Substituting (3.1a) into (3.1b) into (3.1c) and using a Taylor-series expansion of $e^{-\frac{rs_D(x,t)}{K}}$ around $\frac{rs_D(x,t)}{K} = 0$ up to first order, I obtained

$$l(x,t+1) = \gamma l(x,t) + \frac{\beta r}{K}(K - \gamma l(x,t)) \int_{-\infty}^{\infty} k_s(x-y)l(y,t)dy \tag{3.2}$$

We seek travelling wave solutions of (3.2) that propogate to the right with speed $c > 0$ that satisfies

$$l(x,t+1) = l(x-c,t) \tag{3.3}$$

Since (3.2) is linear, we let the edge of the travelling wave be exponential, i.e.,

$$l(x,t) \propto e^{-s_l x} \tag{3.4}$$

with $s_l > 0$, such that (3.2) becomes

$$e^{-s_l x}e^{s_l c} = \gamma e^{-s_l x} + \frac{\beta r}{K}\left(K - \gamma e^{-s_l x}\right)\int_{-\infty}^{\infty} k_s(x-y)e^{-s_l y}dy \tag{3.5}$$

If we now consider annual plants, then $\gamma = 0$, such that

$$e^{s_l c} = \beta r \int_{-\infty}^{\infty} k_s(y-x)e^{-s_l(y-x)}dy \tag{3.6}$$

If we set $v = y - x$, then (3.6) becomes

$$e^{s_l c} = \beta r \int_{-\infty}^{\infty} k_s(v)e^{-s_l v}dv \tag{3.7}$$

Consequently, the travelling wave solution is given by

$$c = \frac{1}{s_l}\ln\left[\beta r M_{k_s}(s_l)\right] \tag{3.8}$$

where, $M_{k_s}(s_l)$ is the moment-generating function of the dispersal kernel (in this the Gaussian distribution with mean 0 and variance σ_p^2). Hence, the travelling wave solution is given by

$$c = \frac{1}{s_l}\ln\left(\beta r e^{0.5 s_l^2 \sigma_s^2}\right). \tag{3.9}$$

This describes a U-shaped relationship between s_l and c. Since the exact value of s_l describing the wave is unknown, solving $\min_{s_l} c$ gives a lower bound for the travelling wave solution, c.

3.2 Numerical results

3.2.1 Parameters used in the simulations

Parameter	Biological interpretation
r	Germination rate
α	Pollen production per plant
β	Maximum seed production per plant
μ	Pollination efficiency
K	Carrying capacity per site
γ_s	Seed survival rate
γ	Plant survival rate
σ_p^2	Pollen dispersal ability
σ_s^2	Seed dispersal ability

Table 3.1: Parameters that were used in the simulation of the invasion dynamics.

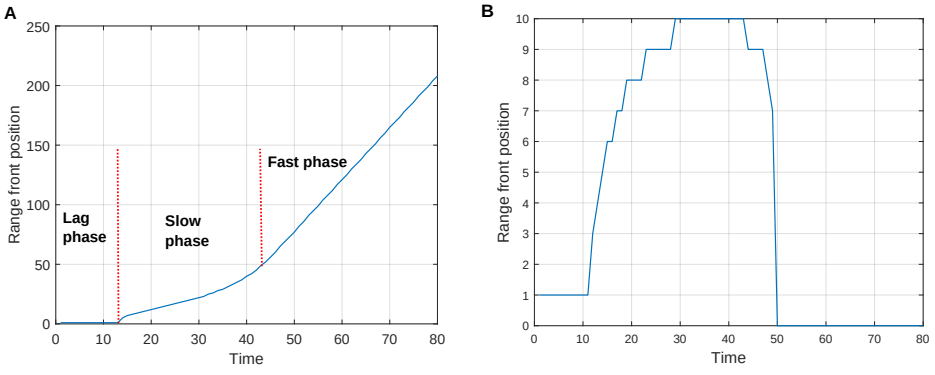


Figure 3.1: **The three phases of the range expansion of a plant population.** Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9, \sigma_p^2 = 50, \sigma_s^2 = 80$ and initial population sizes $s_B(0,0) = 100, l(0,0) = 2$. B shows a boom-and-bust phenomenon. The detection threshold, l^*, is 1. These simulations are based on equations 2.1 to 2.6.

Visual inspection of the curve in Fig. 3.1 suggests a lag, slow and fast phase. Higher detection thresholds resulted in longer lag phases, faster slow phases, but the velocity of the fast phase remained unchanged (see figure A.1 in Appendix A).

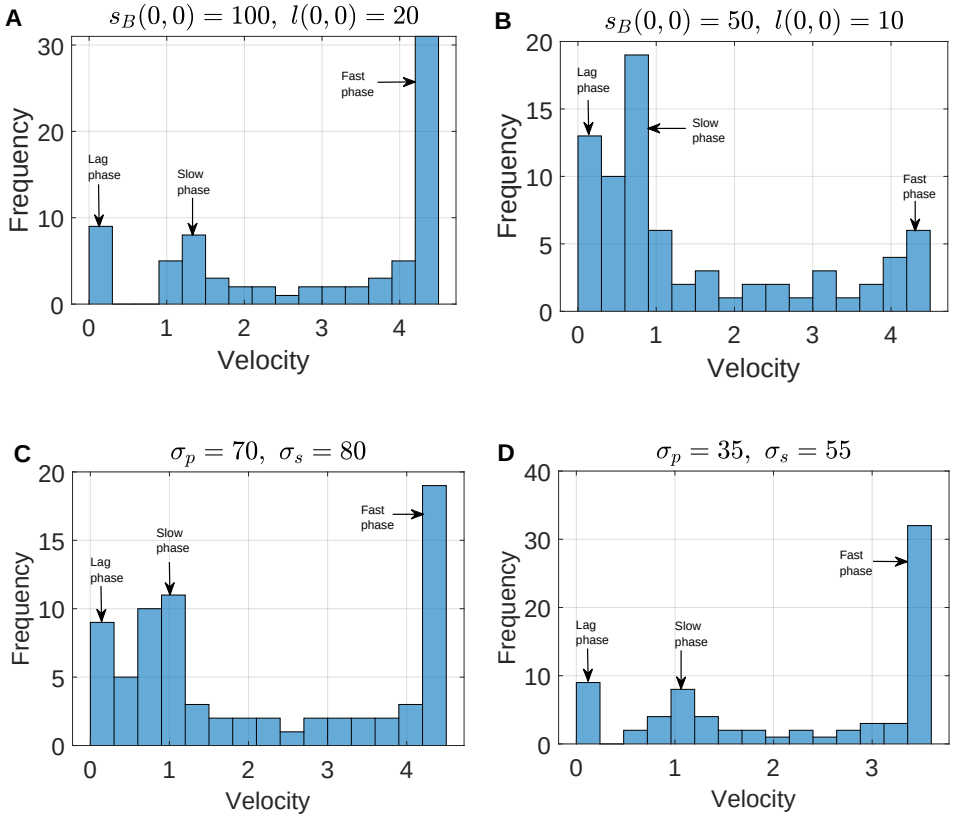


Figure 3.2: **Frequency distributions of the velocity under different initial conditions and dispersal abilities**. Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$, but $\sigma_p = 50$ and $\sigma_s = 80$ in A and B, and $s_B(0,0) = 100$ and $l(0,0) = 2$ in C and D. (A)-(B): Different initial conditions and (C)-(D): Different dispersal abilities. The detection threshold is 1. Each black arrow indicates the bin associated with the lag, slow and fast phase.

The histograms (Fig. 3.2) validate our model based on the range expansion patterns that can be observed: if, with the exception of the lag phase, the bins of the histogram increase in frequency from the left to the right, then the range expansion would be continuously accelerating towards an asymptote, but this is not the case, as we observe a peak between the lag and fast phase, indicating the existence of a slow phase and therefore a biphasic range expansion. Fig. 3.2 depicts the lag, slow and fast phases for four cases. Fig. 3.2A and 3.2B show the influence of the initial conditions on the lag, slow and fast phases: higher initial seeds in the seed bank and plants increase the rate of spread and results in a shorter lag phase and slower fast phase, but the fast phase remains the same. Fig. 3.2C and 3.2D show that a shorter lag phase and faster

slow phase are observed at lower pollen and seed dispersal abilities. All other parameters are identical.

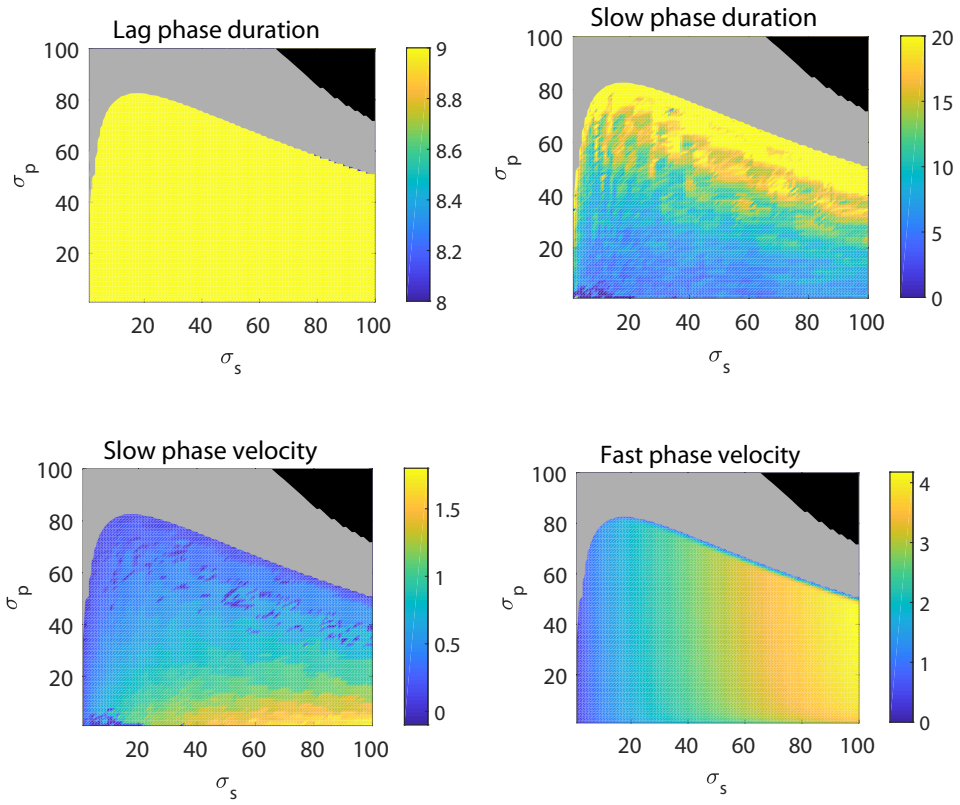


Figure 3.3: **The effect of pollen and seed dispersal ability on the duration of the lag and slow phase, and the velocity of the slow and fast phase to the changes in the pollen and seed dispersal ability.** Parameter values were $r = 0.2, \alpha = 650, \beta = 20, \mu = 0.002, K = 20, \gamma_s = 0.94, \gamma_l = 0.89$. The grey and black regions respectively represent boom-and-bust and extinction, whereas the blue-yellow region represents biphasic range expansion.

We observed three regions in each of the subfigures in Fig. 3.3: (i) lower region with biphasic range expansion, (ii) intermediate region with the boom-and-bust phenomenon and (iii) the top right region with extinction. The boom-and-bust phenomenon can be more clearly seen in the Appendix, Fig. A.3 and A.4, that show the position of the range front and velocity of spread respectively. The boom-and-bust phenomena is shown by the bell shaped curves in Fig. A.3 and the extinction region is shown by the non-bell-shaped

curves in the top right corner where pollen and seed dispersal abilities are the highest.

We observed that the duration of the lag phase increased more with pollen dispersal than with seed dispersal in the biphasic range expansion. The lag phase is even longer when the population enters the boom-and-bust phase (Fig. 3.3A and A.3).

If pollen are dispersed over greater distances, then the rate of spread was actually slower during the initial slow phase of spread (Fig. 3.3C). However, as pollen dispersal distances increased, so did rates of spread during the faster phase of spread (Fig. 3.3D). Increased pollen dispersal resulted in a longer slow phase, whereas shorter pollen dispersal resulted in a shorter slow phase (Fig. 3.3B). The shorter the duration of the slow phase, the higher the velocity thereof, and vice versa (Fig. 3.3B and 3.3C). The duration of the slow phase increases with pollen dispersal ability at a fixed seed dispersal ability, and decreases with increasing seed dispersal ability at a fixed pollen dispersal ability and the opposite effects are seen in the velocity of the slow phase (Fig. 3.3C).

Increased seed dispersal increased both the rate of spread of the slow and fast phase (Fig. 3.3C and D). However, the seed dispersal ability is a stronger driver of the velocity of the fast phase than the pollen dispersal ability. The velocity of the slow and fast phases are lower during the boom-and-bust phase. The velocity of the slow and fast phases decrease as from the biphasic range expansion region to the boom-and-bust region.

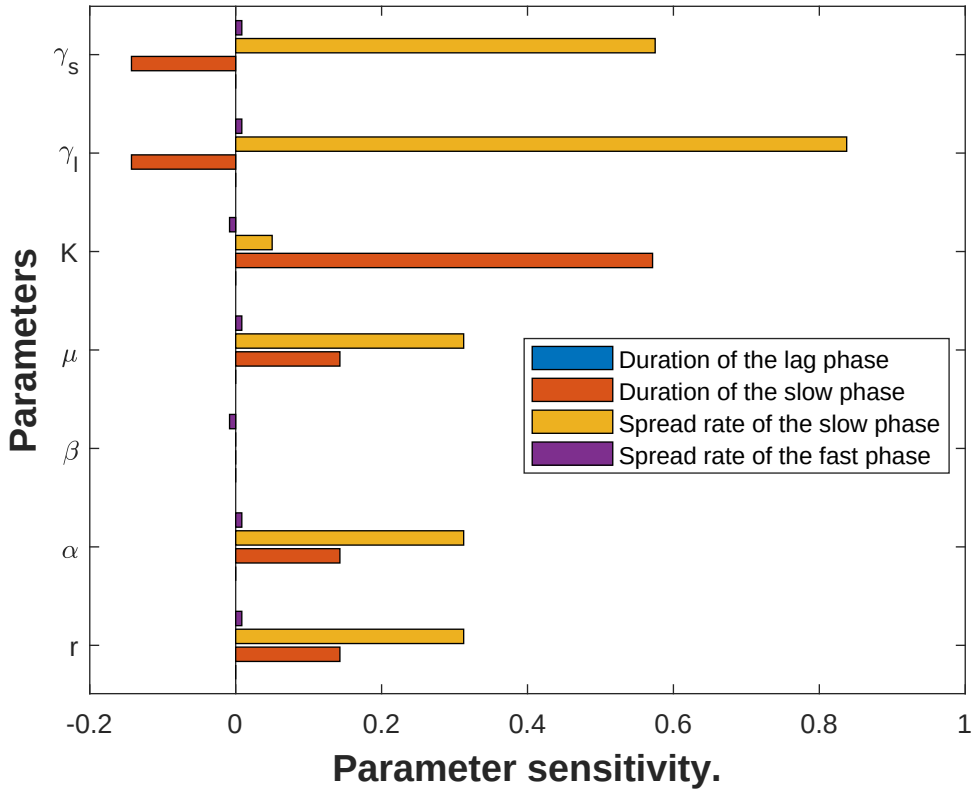


Figure 3.4: **Parameter sensitivity when each of the parameters is increased by 5%.** The sensitivity measures the proportion of change in the parameter values when they are increased by 5% with respect to those in Fig. 3.1. Shown is the sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phase. For this analysis, the duration of the lag phase did not change.

Varying the parameter values did not influence the duration of the lag phase and had very little effect on the velocity of the fast phase (Fig. (3.4)). Increasing γ_l increased velocity of the slow phase the most and increasing K increased the duration of the slow phase the most. Varying the maximum number of ovules per plant, β, had no effect on the duration and velocity of the slow phase. Increased survival rates, γ_s and γ_l, of seeds and plants resulted in a shorter slow phase. K and β decreased the velocity of the fast phase.

Chapter 4

Discussion

4.1 Discussion

The population dynamics of plants with the consideration of the plant life cycle exhibited three regions: (i) a biphasic range expansion, (ii) boom-and-bust and (iii) extinction. In the biphasic range expansion, pollen dispersal ability reduced the velocity of the slow phase and increased the velocity of the fast phase, likely because spread is constrained by seed production in the range core in the slow phase and by seed dispersal at the range front in the fast phase. Seed dispersal had increased the velocity of both the slow and fast phase (see Fig. 3.3). Pollen and seed dispersal decreased the velocity of the slow and phase (Fig. 3.3 C and D). My model produced range expansion with a lag phase and biphasic expansion that consists of a slow initial phase followed by a fast final phase. The biphasic range expansion rather than acellerating range expansion is generally observed for a wide range of pollen and seed dispersal abilities (see Fig. A.2). The complexity of the plant life cycle is such that the relative influence of different life cycle processes can change over the course of invasion as the population grows and spreads across the landscape. I attribute biphasic range expansion in my model to spread rate being constrained differently by seed and pollen dispersal in the slow and fast phase. This provides a novel theoretical explanation for biphasic range expansion, which is a commonly observed empirical phenomenon (Okubo, 1988; Mack, 1981; Mitikka and Hanski, 2010).

An analytical formula for the velocity of plant spread of the full model is not available. However, I derived an analytical formula for the velocity of the fast phase, also known as the asymptotic velocity or travelling wave solution, under unlimited pollination and limited seed dispersal, and the result is given by

$$c = \frac{1}{s_l} \ln \left(\beta r e^{0.5 s_l^2 \sigma_s^2} \right).$$

It is interesting to note that the formula is similar to the classical asymp-

totic velocity of a population with a single kernel:

$$c = \frac{1}{s}\ln[R_0 M(s)]$$

where R_0 is the net reproductive rate, s is a parameter describing the shape of the travelling wave solution and $M(s)$ the moment-generating function of a Gaussian distribution with mean 0 and variance σ^2 (Kot *et al.*, 1996). Our model can therefore be seen as an extention of these previous models. As we could not assess the effect of pollen dispersal on spread rate analytically, we investigated this with simulations.

My model consistently showed a lag phase (Fig. 3.1, 3.2). Changes in pollen and seed dispersal had practically no effect on the lag phase duration during the biphasic range expansion (Fig. 3.3 A). An explanation for the lag phase is pollen limitation in the initial stages when plant density is low. Initial conditions affected the lag phase. A higher initial number of seeds and plants resulted in a shorter lag phase, which is consistent with our expectations, since more seeds and plants initially would speed up the rates of the other life cycle stages, resulting in less time for the population to start spreading. Lower pollen and seed dispersal abilities resulted in a shorter lag phase. This could be because if pollen and seed dispersal abilities are low, the seed production close to the introduction site of the plants is high, resulting in higher plant production near the introduction site of the plants than far from it, and this reduces the time it takes to overcome the Allee effect in pollen supply in the lag phase. Lastly, the duration of the lag phase was not affected by the model parameters in the biphasic range expansion scenario.

In my model, environmental conditions are uniform in space and time. Hence, habitat transition and environmental change do not explain biphasic range expansion in my model, in contrast to explanations given in the literature (Blackburn *et al.*, 2009; Mitikka and Hanski, 2010; Ouyang *et al.*, 2014). My model incorporates a thin- tailed rather than fat tailed dispersal, so stratified dispersal is not an explanation for biphasic range expansion in my model as opposed to previous ones (Shigesada *et al.*, 1996). An Allee effect is implicit in the relationship between the rates of life cycle processes in my model, so changes in the density of the components of the life cycle could generate changes in the velocity of plant spread.

One possible explanation for biphasic range expansion in my model is simply that low pollen production during the slow phase due to small population and low density inhibits seed production and, consequently, reduces the velocity in the slow phase, and when this Allee effect is overcome, the fast phase commences. However, just overcoming an Allee effect is more likely to produce smoothly accelerating velocity of spread, not the observed biphasic spread. The increase in the spread rate of the plants as a result of increased seed dispersal was expected, as plant spread is directly influenced by seed dis-

persal (Allison, 1990). Biphasic range expansion could emerge when different phases are limited by different processes.

Two observations suggest an explanation for biphasic range expansion in my model. Firstly, the effect of seed dispersal ability on the velocity of spread is much stronger for the fast phase than the slow phase, while the effect of pollen dispersal ability is stronger for the slow phase than the fast phase (Figs 3.3C and 3.3 D). This suggests that spread rate in the slow phase is limited mainly by seed production, which depends on pollen dispersal, while the fast phase is more limited by seed dispersal. Secondly, the velocity of the slow phase is negatively related to pollen dispersal ability while velocity of the fast phase is positively related to pollen dispersal ability. This is consistent with an Allee effect through pollen receipt limiting seed production in the slow phase and this Allee effect being overcome in the fast phase.

Plants initially occupy only the leftmost cell in the landscape and as they spread a core part of population with higher density emerges on the left with a range front at lower density on the right. In the slow phase it it likely that increased pollen dispersal, reduces seed production (and hence spread rate) because less of the pollen produced by the population falls in occupied locations (i.e. inside the population range). As the population occupies more of the landscape, increased pollen dispersal ability will result in more pollen dispersal between occupied locations in the population as well as dispersal of pollen to locations at the range front. Locations at the range front have low density so receiving pollen from the core would increase their seed production and therefore increase spread rate. This is likely why the velocity of the fast phase is increased by increasing pollen dispersal ability.

The sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phase to an increase of 5 % in each of the parameters was investigated (Fig. 3.4). The seed and plant survival rate, γ_s and γ, are the only parameters that decreased the duration of the slow phase. Only the carrying capacity, K, and the maximum number of ovules per plant, β, decreased the velocity of the fast phase. This is likely due to a higher carrying capacity, K, and more ovules, β, per plant, that result in higher pollination needed per plant, since pollen are homogeneously distributed over plants. This has a negative impact on seed production further away from the introduction site, which in turn has a negative impact on seed dispersal far from the introduction site and consequently a negative impact on the velocity of plant spread.

Although this model improves our understanding of biphasic range expansions produced by the complex life cycle of plants, my model only considered a single plant species with homogeneous distribution of pollen and seeds over a one-dimensional landscape with homogeneously distributed plants. Since dispersal is often density dependent (Ramanantoanina *et al.*, 2011) and sensitive to habitat (Hui *et al.*, 2012), these can be be incorporated into the model with multiple plant species in future work.

The results showed that seed dispersal is important in both phases of the

biphasic expansion. Pollen dispersal was negatively related to the velocity of the slow phase, but together with seed dispersal was positively related to the velocity of the fast phase. This highlights the importance of pollen dispersal in the range expansion of plant population. This result is in line with published research that emphasises the importance of pollen dispersal as a crucial aspect of the plant life cycle in the range expansion of plant populations (Howe *et al.*, 1988; Starfinger and Stöcklin, 1996). It is therefore important for ecologists to consider the full life cycle of plants in studying and explaining patterns in range expansions.

Appendices

Appendix A

Supplementary figures

A.1 Range expansion and velocity of spread

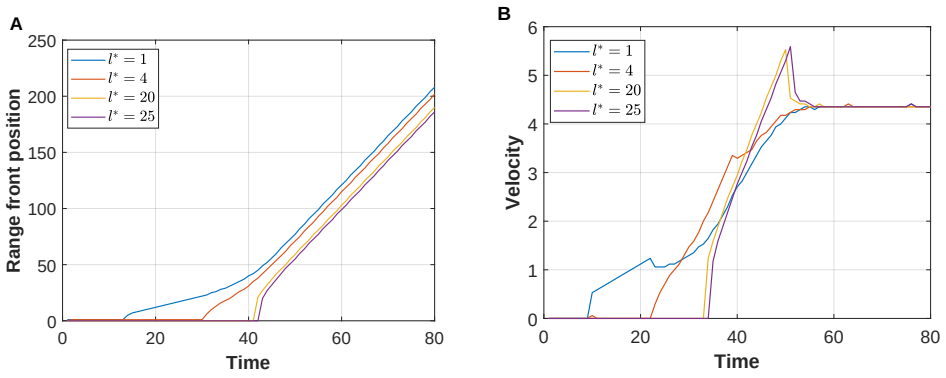
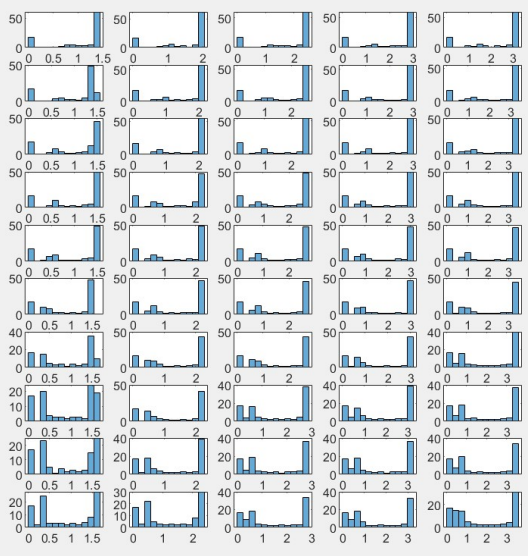


Figure A.1: **Range expansion and spread rate for different detection thresholds**. Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$. The slow phase is sensitive to the detection threshold, but not the fast phase or asymptotic spread rate.

A.2 Histograms for a wide range of σ_p and σ_s.



(a) $\sigma_p = 10 : 10 : 100,\ \sigma_s = 10 : 10 : 50$

(b) $\sigma_p = 10 : 10 : 100,\ \sigma_s = 60 : 10 : 100$

Figure A.2: **Histogram plots for** $\sigma_p = 10 : 10 : 100$ **and** $\sigma_s = 10 : 10 : 100$. Parameter values were $r = 0.1, \alpha = 3000, \beta = 500, \mu = 0.001, K = 30, \gamma_s = 0.95, \gamma_l = 0.9$. These histograms validate the existence of the slow phase. Horizontal axis: velocity and vertical axis: frequency.

A.3

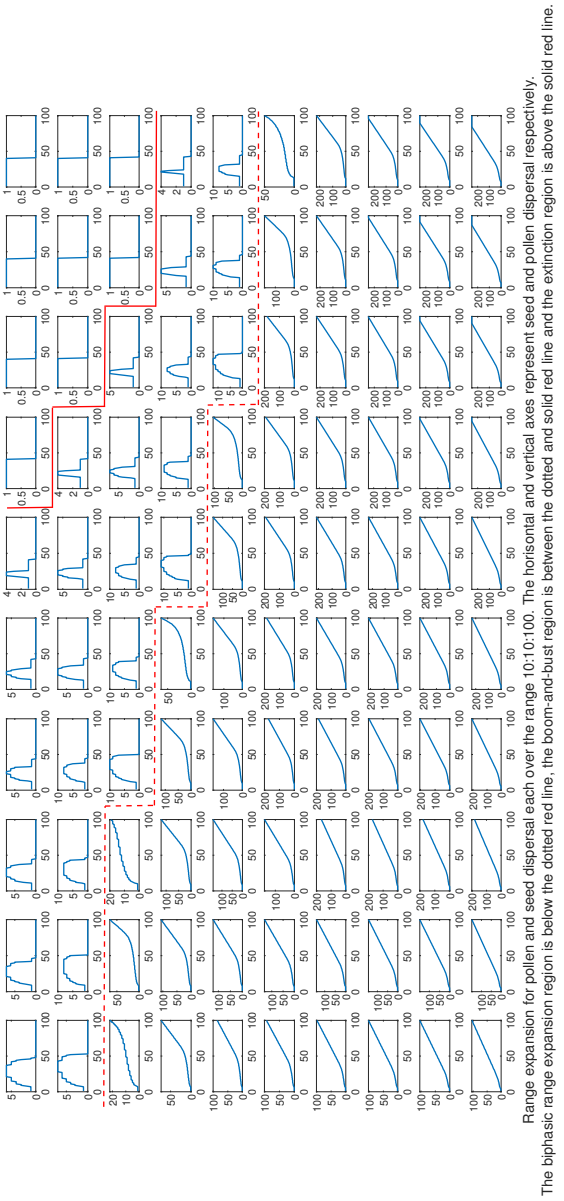


Figure A.3

A.4

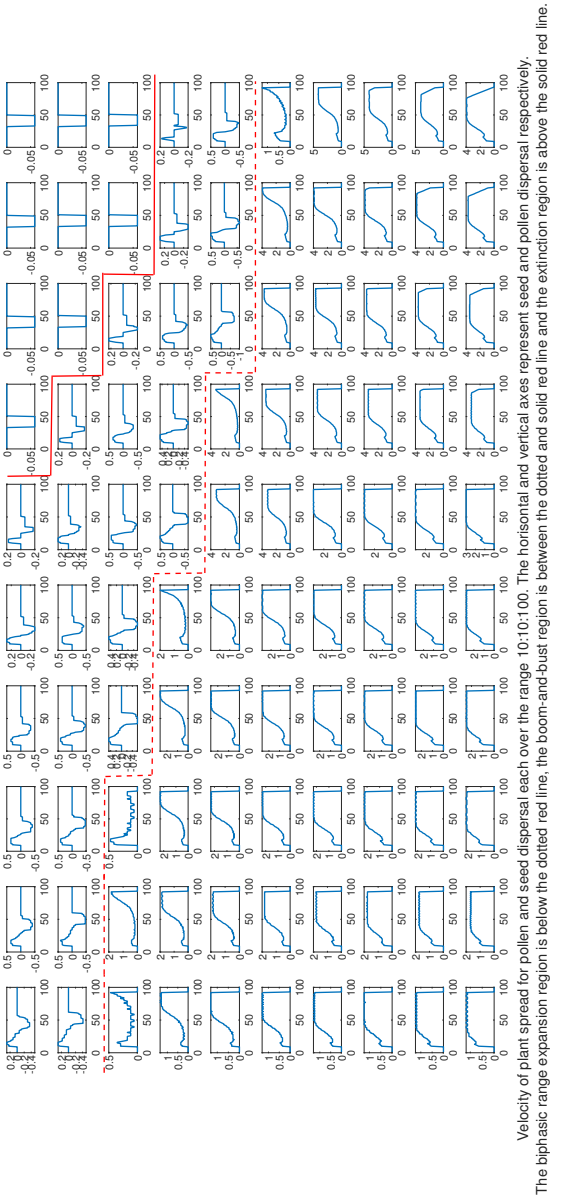


Figure A.4

A.5 Sensitivity analysis with a detection threshold of $l^* = 0.95$ and each of the parameters in table 3.1.

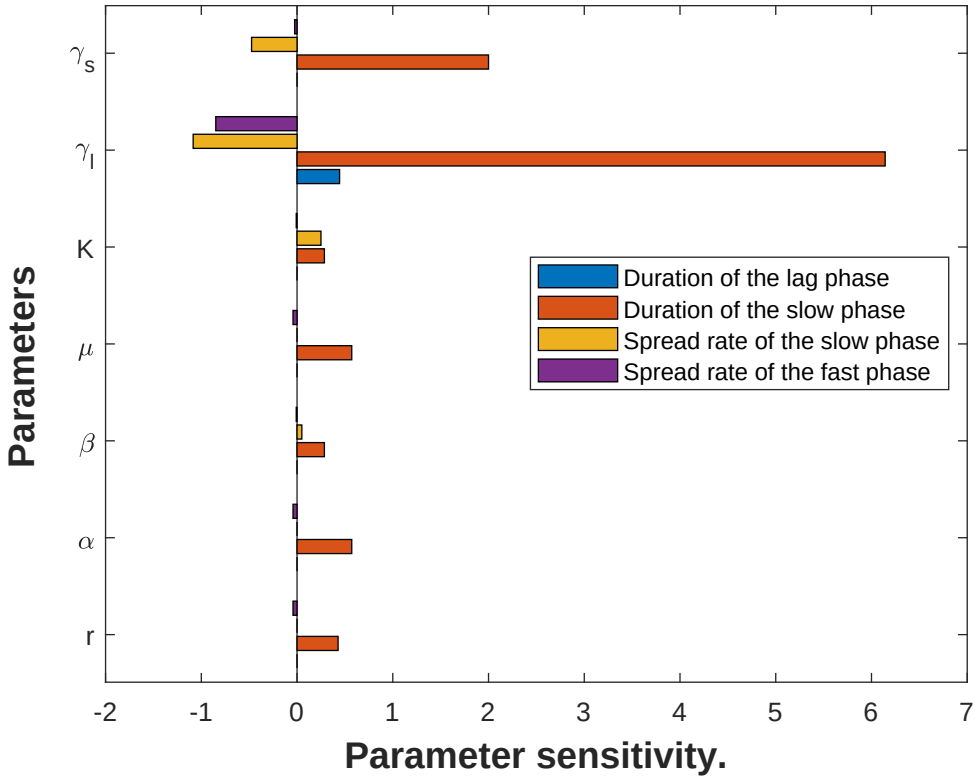


Figure A.5: **Parameter sensitivity when each of the parameters is decreased by 5% and the detection threshold, l^*, is 0.95.** The sensitivity measures the proportion of change in the parameter values when they are decreased by 5% with respect to those in Fig. 3.1. Shown is the sensitivity of the duration of the lag and slow phase, and the velocity of the slow and fast phase. For this analysis, the duration of the lag phase did not change. Only γ_l, the plant survival rate, increased the duration of the lag phase. The decrease of 5% of the detection threshold and decrease of 5% in γ_s resulted in an almost 200% longer duration of the slow phase. The 5% decrease in γ_l and the detection threshold resulted in a staggering 600% increase in the duration of the lag phase and a 100% decrease in the spread rate of the slow phase.

A.6 MATLAB code for Fig. A.1 A and B

```
close all

X = 250;
% Size of landscape (cells)
T = 100;
% Number of generations.
l = zeros(X,T);
% Matrix storing plant density at each location.
p = zeros(X,T);
% Matrix storing pollen produced at each location.
pd = zeros(X,T);
% Matrix storing pollen dispersed to each location.
s = zeros(X,T);
% Matrix storing seeds produced at each location.
sd = zeros(X,T);
% Matrix storing seeds dispersed to each location.
sB = zeros(X,T);
% Matrix storing seeds in seed bank at each location.
r = 0.1;
% Germination rate of seeds dispersed to a location
alpha = 3000;
% Number of pollen grains produced per plant
beta = 500;
% Maximum number of ovules per plant
mu = 0.001;
% Shape parameter
K = 30;
% Carrying capacity of total number of plants at each location x
gamma_l = 0.9;
% Survival rate of plants from generation t to generation t+1
gamma_s = 0.95;
% Survival rate of seeds from generation t to generation t+1;

% Initial number of seeds in the seed bank
sB(1,1) = 100;
% Initial number of plants
l(1,1) = 2;

% DP and DS are the pollen and seed dispersal kernels respectively.
DP = zeros(X+1);
DS = zeros(X+1);
```

```
% Set variance of pollen dispersal kernel
vp = 50;
% Set variance of seed dispersal kernel
vs = 80;


syms d;
GaussP = (2/(sqrt(2*pi*vp)))*exp((-d^2)/(2*vp));
GaussS = (2/(sqrt(2*pi*vs)))*exp((-d^2)/(2*vs));
GaussP_evaluate = int(GaussP,d);
GaussS_evaluate = int(GaussS,d);


% Analytical integration
for x = 1:X+1
    DP(x) = eval(subs(GaussP_evaluate,d,x)-...
    subs(GaussP_evaluate,d,(x-1)));
    DS(x) = eval(subs(GaussS_evaluate,d,x)-...
     subs(GaussS_evaluate,d,(x-1)));
end


for t = 2:T

    for x = 1:X
        % Compute the number of pollen grains produced at
        % each location.
        p(x,t-1) = alpha*l(x,t-1);
    end

    for x = 1:X
        for y = 1:X
            % Compute the the number of pollen grains
            % at each location post dispersal.
            pd(x,t-1) = pd(x,t-1) + DP(abs(x-y)+1)*p(y,t-1);
        end
    end

    for x = 1:X
        % Compute the seeds produced at each location.
        s(x,t-1) = beta*l(x,t-1)*(1-exp(-(mu*pd(x,t-1))/(beta*K)));
    end
```

```
    for x = 1:X
        for y = 1:X
            % Compute the number of seeds at each
            % location after dispersal.
            sd(x,t-1) = sd(x,t-1) + DS(abs(x-y)+1)*s(y,t-1);
        end
    end

    for x = 1:X
        % Compute the number of seeds in the seed bank at
        % each location.
        sB(x,t) = gamma_s*(1-r)*(sB(x,t-1)+...
                                 sd(x,t-1));
    end

    for x = 1:X
        % Compute the number of plants at each location.
        l(x,t) = K - (K-gamma_l*l(x,t-1))*exp(-(r*(sB(x,t-1)+...
                              sd(x,t-1))/K));
    end

end

% Vector for storing plants at range front
R = zeros(1,T);

set(0, 'DefaultLineLineWidth', 1);
% Detection thresholds
L = [1,4,20,25];

% The t values at which the range
% expansion starts for each detection threshold.
tstart = [15 36 43 44];
% tstart = 15;

for k = 1:length(L)
    % Vector for storing the position values for
    % each detection threshold
    P_k = zeros(1,T);
    % Store instantaneous spread rate of plants in S_instant_k for
    % each detection threshold.
    S_instant_k = zeros(1,T);

    for t = 1:T
```

```
        for x = 1:X
            % The range front is the last location
            % where the number of plants
            % exceeds the detection threshold.
            if l(x,t) >= L(k)
                R(t) = l(x,t);
                P_k(t) = x;
            end
        end
    end

    figure(2)
    plot(P_k(1:80))
    grid on
    ax = gca;
    ax.FontSize = 15;
    xlabel('Time','FontSize',15)
    ylabel('Range front position','FontSize',15)
    % grid on
    hold on
    leg1 = legend('$l^{*} = 1$', '$l^{*} = 4$', '$l^{*} = 20$',
                                                '$l^{*} = 25$');
    set(leg1,'Interpreter','latex')


    %for t = tstart(k):T-8
    for t = 10:T-8
        %S_instant_k(s) = P_k(s)-P_k(s-1);
        S_instant_k(t) = ((P_k(t)-P_k(t-1))+(P_k(t+1)-P_k(t))+(P_k(t-1)
        -...P_k(t-2)) + (P_k(t+2)-P_k(t+1))+...
            (P_k(t-2)-P_k(t-3))+(P_k(t-3)-P_k(t-4))+---
            (P_k(t+3)-P_k(t+2))+(P_k(t+4)-...
            P_k(t+3))+(P_k(t-4)-P_k(t-5))+...
            (P_k(t+5)-P_k(t+4))+(P_k(t-5)-...
            P_k(t-6))+(P_k(t+6)-P_k(t+5))+(P_k(t-6) -...
            P_k(t-7))+(P_k(t-7)-P_k(t-8))+...
            (P_k(t+7)-P_k(t+6))+(P_k(t+8)-...
            P_k(t+7))+(P_k(t-8)-P_k(t-9)))/17;
    end


    % Plot the instantaneous spread rate
    figure(3)
    plot(S_instant_k(1:80))
```

```
    grid on
    %xlim([tstart(1) T-8])
    %xlim([tstart(1) 63])
    hold on
    leg1 = legend('$l^{*} = 1$', '$l^{*} = 4$', '$l^{*} = 20$',
                                                '$l^{*} = 25$');
    set(leg1,'Interpreter','latex')
    xlabel('Time','FontSize',12), ylabel('Spread rate')
    legend('l* = 1','l* = 4','l* = 15','l* = 22')
    %legend('l* = 1','l* = 2')
    ax = gca;
    ax.FontSize = 15;

    % Histogram of spread rate with 15 bins
    figure(4)
    histogram(S_instant_k(1:85),15)
    grid on
    ax = gca;
    ax.FontSize = 14;
    opskrif = title('$\sigma_p = 80,\ \sigma_s = 70$');
    set(opskrif,'Interpreter','latex')
    %text(0,1,'Units','normalized')
end
```

A.7 MATLAB code for Fig. 3.3 A - D.

```
close all

X = 250;
% Size of landscape (cells)
T = 100;
% Number of generations.
l = zeros(X,T);
% Matrix storing plant density at each location.
p = zeros(X,T);
% Matrix storing pollen produced at each location.
pd = zeros(X,T);
% Matrix storing pollen dispersed to each location.
s = zeros(X,T);
% Matrix storing seeds produced at each location.
sd = zeros(X,T);
% Matrix storing seeds dispersed to each location.
sB = zeros(X,T);
% Matrix storing seeds in seed bank at each location.
```

```
r = 0.1;
% Germination rate of seeds dispersed to a location
alpha = 3000;
% Number of pollen grains produced per plant
beta = 500;
% Maximum number of ovules per plant
mu = 0.001;
% Shape parameter
K = 30;
% Carrying capacity of total number of plants at each location x
gamma_l = 0.9;
% Survival rate of plants from generation t to generation t+1
gamma_s = 0.95;
% Survival rate of seeds from generation t to generation t+1;

%DP and DSp are the pollen and seed dispersal kernels respectively.
DP = zeros(X+1);
DS = zeros(X+1);

% Pollen and seed variances from 1 in intervals of 1 to 100.
var_p = 1:100;
var_s = 1:100;


bins = 15;

syms d;

Lag_duration = zeros(length(var_p),length(var_s));
slowphase_duration = zeros(length(var_p),length(var_s));
Slowphase_spreadrate = zeros(length(var_p),length(var_s));
Fastphase_spreadrate = zeros(length(var_p),length(var_s));
Time_to_asymptspread = zeros(length(var_p),length(var_s));
average_before_asymptspread = zeros(length(var_p),length(var_s));
distance_to_asymptspread = zeros(length(var_p),length(var_s));

%Store plants at range front
R = zeros(1,T);
%Store values of range front
P_k = zeros(1,T);


for vp = 1:100
    for vs = 1:100
```

```
var_p = 1:100;
var_s = 1:100;

% Reset matrices after each set of runs.
l = zeros(X,T);
p = zeros(X,T);
pd = zeros(X,T);
s = zeros(X,T);
sd = zeros(X,T);
sB = zeros(X,T);

% Initial number of seeds in the seed bank
sB(1,1) = 100;
% Initial number of plants
l(1,1) = 2;

if vp==0 || vs == 0
    continue
else
    GaussP = (2/(sqrt(2*pi*vp)))*exp((-d^2)/(2*vp));
    GaussS = (2/(sqrt(2*pi*vs)))*exp((-d^2)/(2*vs));
    GaussP_evaluate = int(GaussP,d);
    GaussS_evaluate = int(GaussS,d);
end

for x = 1:X+1
    if vp==0 || vs == 0
        DP(x)=0;
        DS(x)=0;
    else
        DP(x) = eval(subs(GaussP_evaluate,d,x)-...
        subs(GaussP_evaluate,d,(x-1)));
        DS(x) = eval(subs(GaussS_evaluate,d,x)-...
        subs(GaussS_evaluate,d,(x-1)));
    end
end

for t = 2:T


    for x = 1:X
        % Compute the number of pollen produced
```

```
            %at each location.

            p(x,t-1) = alpha*l(x,t-1);
        end

        for x = 1:X
            %pd(x,t)=0;
            for y = 1:X
                % Compute the number of pollen at each location
                % after dispersal.
                pd(x,t-1) = pd(x,t-1) + DP(abs(x-y)+1)*p(y,t-1);
            end
        end

        for x = 1:X
            % Compute the seeds produced at each location.
            s(x,t-1) = beta*l(x,t-1)*(1-...
                                    exp(-(mu*pd(x,t-1))/(beta*K)));
        end

        for x = 1:X
            for y = 1:X
                % Compute the number of seeds at
                % each location after dispersal.
                sd(x,t-1) = sd(x,t-1) + DS(abs(x-y)+1)*s(y,t-1);
            end
        end

        for x = 1:X
            % Compute the number of seeds at each location in the
            % seed bank.
            sB(x,t) = gamma_s*(1-r)*(sB(x,t-1)+sd(x,t-1));
        end

        for x = 1:X
            % Compute the number of plants at each location.
            l(x,t) = K - (K-gamma_l*l(x,t-1))*exp(-(r*(sB(x,t-1)+.
                                                    sd(x,t-1))/K));
        end
    end

    set(0, 'DefaultLineLineWidth', 1);
    % Detection threshold of 1 used in simulations.
    L = 1;
```

```
for k = 1:length(L)
    %   Store range front positions in P_k
    P_k = zeros(1,T);
    %  Store instantaneous spread rate of plants in
    % S_instant_k
    S_instant_k = zeros(1,T);
    for t = 1:T
        for x = 1:X
            % The range front is the last location where the
            % number of plants exceeds the detection
            % threshold of L.
            if l(x,t) >= L(k)
                R(t) = l(x,t);
                P_k(t) = x;
            end
        end
    end


    for t = 10:T-8
        S_instant_k(t) = ((P_k(t)-P_k(t-1))+(P_k(t+1)-P_k(t))+
        (P_k(t-1)-P_k(t-2))+(P_k(t+2)-P_k(t+1))+...
        (P_k(t-2)-P_k(t-3))+(P_k(t-3)-P_k(t-4))+...
        (P_k(t+3)-P_k(t+2))+(P_k(t+4)-P_k(t+3))+...
        (P_k(t-4)-P_k(t-5))+...
        (P_k(t+5)-P_k(t+4))+(P_k(t-5)-P_k(t-6))+...
        (P_k(t+6)-P_k(t+5))+(P_k(t-6)-P_k(t-7))+...
        (P_k(t-7)-P_k(t-8))+...
        (P_k(t+7)-P_k(t+6))+(P_k(t+8)-P_k(t+7))+...
        (P_k(t-8)-P_k(t-9)))/17;
    end


    %Compute the asymptotic spread rate.
    Fastphase_spreadrate(find(var_p==vp),find(var_s==vs)) =
max(S_instant_k);

    % Heat maps of the duration of lag and slow phase.
[N_lag, EDGES_lag] = histcounts(S_instant_k(1:45),bins);
    Lag_duration(find(var_p==vp),find(var_s==vs)) = N_lag(1);

[N_slowphase_dur,EDGES_slowphase_dur] =
 histcounts(S_instant_k(S_instant_k<0.9*...
```

```
 Fastphase_spreadrate(find(var_p==vp),find(var_s==vs))),bins);
            pks_slowphase_dur = findpeaks(N_slowphase_dur);
      if isempty(pks_slowphase_dur)
                % Put spread rate equal to zero if there are no peaks
          slowphase_duration(find(var_p==vp),find(var_s==vs))=0;
          Slowphase_spreadrate(find(var_p==vp),find(var_s==vs))=0;

      else
          slowphase_duration(find(var_p==vp),find(var_s==vs)) =
max(unique(pks_slowphase_dur));
                % If more than one edge (ie, more than one spread rate)
                % has the same frequency, we choose the lower of these
                % values as the spread rate of the slow phase.

Slowphase_spreadrate(find(var_p==vp),find(var_s==vs))=...
min(EDGES_slowphase_dur(N_slowphase_dur==max(unique(pks_slowphase_dur))
      end

%               Lag_duration
%               slowphase_duration
%               Slowphase_spreadrate
%               Fastphase_spreadrate


            % Find the minimum t-value that corresponds to the velocity
            t_before_asymtspread =
 min(find(S_instant_k == max(S_instant_k(:))));

            Time_to_asymptspread(find(var_p==vp),find(var_s==vs)) =
 t_before_asymtspread ;
      average_before_asymptspread(find(var_p==vp),find(var_s==vs)) =
 mean(S_instant_k(1:t_before_asymtspread));
 distance_to_asymptspread(find(var_p==vp),find(var_s==vs)) =
  P_k(t_before_asymtspread);

        end
    end
end

figure(1)
pcolor(Fastphase_spreadrate)
shading('interp')
ax = gca;
ax.FontSize = 14;
```

```
ay.FontSize = 14;
xlabel('\sigma_s','FontSize',14)
ylabel('\sigma_p','FontSize',14)
colorbar
cbh=colorbar('v');
set(cbh,'YTick',0:1:5)

figure(2)
pcolor(Slowphase_spreadrate)
shading('interp')
ax = gca;
ax.FontSize = 14;
ay.FontSize = 14;
xlabel('\sigma_s','FontSize',14)
ylabel('\sigma_p','FontSize',14)
colorbar

figure(3)
pcolor(Lag_duration)
shading('interp')
ax = gca;
ax.FontSize = 14;
ay.FontSize = 14;
xlabel('\sigma_s','FontSize',14)
ylabel('\sigma_p','FontSize',14)
colorbar
cbh=colorbar('v');
set(cbh,'YTick',9:2:11)

figure(4)
pcolor(slowphase_duration)
shading('interp')
ax = gca;
ax.FontSize = 14;
ay.FontSize = 14;
xlabel('\sigma_s','FontSize',14)
ylabel('\sigma_p','FontSize',14)
colorbar
```

List of References

Allee, W. (1931). Animal aggregations: a study in general sociology. á univ.

Allison, T.D. (1990). Pollen production and plant density affect pollination and seed production in taxus canadensis. *Ecology*, vol. 71, no. 2, pp. 516–522.

Ashman, T.-L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M.O., Mazer, S.J., Mitchell, R.J. *et al.* (2004). Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, vol. 85, no. 9, pp. 2408–2421.

Blackburn, T.M., Lockwood, J. and Cassey, P. (2009). *Avian invasions: the ecology and evolution of exotic birds*. Oxford University Press.

Branco, J., Ferreira, J. and De Oliveira, P. (2007). Numerical methods for the generalized fisher–kolmogorov–petrovskii–piskunov equation. *Applied Numerical Mathematics*, vol. 57, no. 1, pp. 89–102.

Bullock, J.M., Pywell, R.F. and Coulson-Phillips, S.J. (2008). Managing plant population spread: prediction and analysis using a simple model. *Ecological Applications*, vol. 18, no. 4, pp. 945–953.

Carlsson, N.O., Sarnelle, O. and Strayer, D.L. (2009). Native predators and exotic prey–an acquired taste? *Frontiers in Ecology and the Environment*, vol. 7, no. 10, pp. 525–532.

Clark, J.S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, vol. 152, no. 2, pp. 204–224.

Crooks, J.A., Soulé, M.E. and Sandlund, O. (1999). Lag times in population explosions of invasive species: causes and implications. *Invasive species and biodiversity management*, vol. 103, p. 125.

Davis, H.G., Taylor, C.M., Lambrinos, J.G. and Strong, D.R. (2004). Pollen limitation causes an allee effect in a wind-pollinated invasive grass (spartina alterniflora). *Proceedings of the National Academy of Sciences*, vol. 101, no. 38, pp. 13804–13807.

Fisher, R.A. (1937). The wave of advance of advantageous genes. *Annals of eugenics*, vol. 7, no. 4, pp. 355–369.

Gleaves, J. (1973). Gene flow mediated by wind-borne pollen. *Heredity*, vol. 31, no. 3, p. 355.

Groves, R. (2006). Are some weeds sleeping? some concepts and reasons. *Euphytica*, vol. 148, no. 1-2, pp. 111–120.

Harrison, J. and Cherry, M. (1997). *The atlas of southern African birds*, vol. 1. BirdLife South Africa Johannesburg.

Hawkes, C.V. (2007). Are invaders moving targets? the generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist*, vol. 170, no. 6, pp. 832–843.

Hiddink, J.G., Burrows, M.T. and García Molinos, J. (2015). Temperature tracking by north sea benthic invertebrates in response to climate change. *Global change biology*, vol. 21, no. 1, pp. 117–129.

Higgins, S.I. and Richardson, D.M. (1999). Predicting plant migration rates in a changing world: the role of long-distance dispersal. *The American Naturalist*, vol. 153, no. 5, pp. 464–475.

Horak, J., Hui, C., Roura-Pascual, N. and Romportl, D. (2013). Changing roles of propagule, climate, and land use during extralimital colonization of a rose chafer beetle. *Naturwissenschaften*, vol. 100, no. 4, pp. 327–336.

Howe, H.F., Westley, L.C. *et al.* (1988). *Ecological relationships of plants and animals.* Oxford University Press.

Hui, C. and Richardson, D.M. (2017). *Invasion dynamics.* Oxford University Press.

Hui, C., Roura-Pascual, N., Brotons, L., Robinson, R.A. and Evans, K.L. (2012). Flexible dispersal strategies in native and non-native ranges: environmental quality and the ?good–stay, bad–disperse?rule. *Ecography*, vol. 35, no. 11, pp. 1024–1032.

Hulme, P.E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of applied ecology*, vol. 46, no. 1, pp. 10–18.

Kot, M., Lewis, M.A. and van den Driessche, P. (1996). Dispersal data and the spread of invading organisms. *Ecology*, vol. 77, no. 7, pp. 2027–2042.

Lewis, M.A., Petrovskii, S.V. and Potts, J.R. (2016). *The mathematics behind biological invasions*, vol. 44. Springer.

Lucie Hemrová, James M. Bullock, D.A.P.H.S.M.W.Z.M. (2017). Drivers of plant species' potential to spread: the importance of demography versus seed dispersal.

Mack, R.N. (1981). Invasion of bromus tectorum l. into western north america: an ecological chronicle. *Agro-ecosystems*, vol. 7, no. 2, pp. 145–165.

Malanson, G.P. and Rodriguez, N. (2018). Traveling waves and spatial patterns from dispersal on homogeneous and gradient habitats. *Ecological complexity*, vol. 33, pp. 57–65.

McGeoch, M.A. and Latombe, G. (2016). Characterizing common and range expanding species. *Journal of Biogeography*, vol. 43, no. 2, pp. 217–228.

Mitikka, V. and Hanski, I. (2010). Pgi genotype influences flight metabolism at the expanding range margin of the european map butterfly. In: *Annales Zoologici Fennici*, vol. 47, pp. 1–14. BioOne.

Mitikka, V., Heikkinen, R.K., Luoto, M., Araújo, M.B., Saarinen, K., Pöyry, J. and Fronzek, S. (2008). Predicting range expansion of the map butterfly in northern europe using bioclimatic models. *Biodiversity and Conservation*, vol. 17, no. 3, pp. 623–641.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, vol. 105, no. 49, pp. 19052–19059.

Nathan, R., Klein, E., Robledo-Arnuncio, J.J. and Revilla, E. (2012). Dispersal kernels. In: *Dispersal ecology and evolution*, pp. 187–210. Oxford University Press Oxford.

Nathan, R., Safriel, U.N. and Noy-Meir, I. (2001). Field validation and sensitivity analysis of a mechanistic model for tree seed dispersal by wind. *Ecology*, vol. 82, no. 2, pp. 374–388.

Okubo, A. (1980). Diffusion and ecological problems:(mathematical models). *Biomathematics*.

Okubo, A. (1988). Diffusion-type models for avian range expansion. In: *Acta XIX congress internationalis ornithologici*, vol. 1, pp. 1038–1049. National Museum of Natural Sciences, University of Ottawa Press.

Ouyang, F., Hui, C., Ge, S., Men, X.-Y., Zhao, Z.-H., Shi, P.-J., Zhang, Y.-S. and Li, B.-L. (2014). Weakening density dependence from climate change and agricultural intensification triggers pest outbreaks: a 37-year observation of cotton bollworms. *Ecology and evolution*, vol. 4, no. 17, pp. 3362–3374.

Ramanantoanina, A. and Hui, C. (2016). Formulating spread of species with habitat dependent growth and dispersal in heterogeneous landscapes. *Mathematical biosciences*, vol. 275, pp. 51–56.

Ramanantoanina, A., Hui, C. and Ouhinou, A. (2011). Effects of density-dependent dispersal behaviours on the speed and spatial patterns of range expansion in predator–prey metapopulations. *Ecological modelling*, vol. 222, no. 19, pp. 3524–3530.

Rouget, M., Robertson, M.P., Wilson, J.R., Hui, C., Essl, F., Renteria, J.L. and Richardson, D.M. (2016). Invasion debt–quantifying future biological invasions. *Diversity and Distributions*, vol. 22, no. 4, pp. 445–456.

Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. and Nathan, R. (2018). Long-distance seed dispersal. *Annual Plant Reviews online*, pp. 204–237.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M. *et al.* (2017). No saturation in the accumulation of alien species worldwide. *Nature communications*, vol. 8, p. 14435.

Shigesada, N., Kawasaki, K. and Takeda, Y. (1996). Modeling stratified diffusion in biological invasions. *Oceanographic Literature Review*, vol. 2, no. 43, pp. 168–169.

Simberloff, D. and Gibbons, L. (2004). Now you see them, now you don't!–population crashes of established introduced species. *Biological Invasions*, vol. 6, no. 2, pp. 161–172.

Skellam, J.G. (1951). Random dispersal in theoretical populations. *Biometrika*, vol. 38, no. 1/2, pp. 196–218.

Starfinger, U. and Stöcklin, J. (1996). Seed, pollen, and clonal dispersal and their role in structuring plant populations. In: *Progress in Botany/Fortschritte der Botanik*, pp. 336–355. Springer.

Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. (1999). What is the allee effect? *Oikos*, pp. 185–190.

Wang, M.-H. and Kot, M. (2001). Speeds of invasion in a model with strong or weak allee effects. *Mathematical biosciences*, vol. 171, no. 1, pp. 83–97.

Weinberger, H.F. (1982). Long-time behavior of a class of biological models. *SIAM journal on Mathematical Analysis*, vol. 13, no. 3, pp. 353–396.

Williamson, M. and Griffiths, B. (1996). *Biological invasions*. Springer Science & Business Media.

Williamson, M., Pyšek, P., Jarošík, V. and Prach, K. (2005). On the rates and patterns of spread of alien plants in the czech republic, britain, and ireland. *Ecoscience*, vol. 12, no. 3, pp. 424–433.

Wingfield, M.J., Roux, J. and Wingfield, B.D. (2011). Insect pests and pathogens of australian acacias grown as non-natives–an experiment in biogeography with far-reaching consequences. *Diversity and Distributions*, vol. 17, no. 5, pp. 968–977.